Habitat requirements and dispersal ability of the Spanish Fritillary (Euphydryas desfontainii) in southern Portugal: evidence-based conservation suggestions for an endangered taxon

Pennekamp, Frank ; Garcia-Pereira, Patrícia ; Schmitt, Thomas

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ORIGINAL PAPER

Habitat requirements and dispersal ability of the Spanish Fritillary (*Euphydryas desfontainii*) in southern Portugal: evidence-based conservation suggestions for an endangered taxon

Frank Pennekamp · Patrícia Garcia-Pereira · Thomas Schmitt

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Abstract A high level of plant and insect diversity, and more specifically high butterfly diversity characterizes the Mediterranean Basin. However, alarming negative trends have been reported for butterfly populations in that region emphasizing the urgent need to better understand the drivers of their population declines. Habitat specialists of grasslands are strongly affected, mainly by land use change and climate change. Thorough assessments of habitat requirements and dispersal abilities are crucial to establish appropriate conservation measures to counter these threats. Here, we investigate the ecological requirements and dispersal ability of *Euphydryas desfontainii,* one of Portugal's rarest butterflies, to develop targeted conservation strategies. The assessment of habitat requirements showed differences between occupied and unoccupied patches in terms of host plant abundance and area. Mark–release–recapture data were used to model demographic parameters: survival rates decreased linearly over the flight period and recruitment followed a parabolic curve with separate peaks for males and females. The movement data were fitted to an inverse power function and used to predict the probability of long-distance dispersal. The obtained probabilities were compared to related checkerspot butterflies and interpreted regarding the structural connectivity of the investigated habitat network. We suggest focusing on the preservation of remaining habitat patches, whilst monitoring and safeguarding that their vegetation structure does provide sufficiently diversified microclimates in order to best conserve *E.desfontainii* populations.

Keywords Connectivity · Dispersal kernel · Habitat quality · Mark–release–recapture · Mediterranean region · Metapopulation

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F. Pennekamp
Earth and Life Institute, Université Catholique de Louvain, Louvain-la-Neuve, Belgium

F. Pennekamp · T. Schmitt
Department of Biogeography, Trier University, Trier, Germany

F. Pennekamp (✉)
Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland
e-mail: Frank.Pennekamp@ieu.uzh.ch

P. Garcia-Pereira
National Museum of Natural History and Science, Lisbon, Portugal

T. Schmitt
Senckenberg German Entomological Institute, Müncheberg, Germany

T. Schmitt
Zoology, Faculty of Natural Science I, Institute of Biology, Martin-Luther-University Halle-Wittenberg, Halle, Germany

Introduction

The Mediterranean Basin harbours an enormous biological diversity positioning it among the most important global biodiversity hotspots (Myers et al. 2000). High plant species richness and endemism (Médail and Quézel 1999) in combination with its role as glacial refugium (Hewitt 2011) have resulted in elevated numbers of insect species, with butterflies as one example (Dennis and Schmitt 2009). However, this diversity is at risk because habitat conversion largely exceeds habitat protection in the Mediterranean region (Hoekstra et al. 2005). This development is likely to

lead to large-scale species extinctions if not counteracted by efficient conservation measures (Hoekstra et al. 2005). Although long-term data on population trends are only available for few Mediterranean regions (Stefanescu et al. 2011a), recent findings from the butterfly monitoring program in Catalonia and Andorra show alarming trends for butterflies, especially those inhabiting open habitat types such as shrub- and grasslands (Stefanescu et al. 2011b). Confirming the findings from other geographic areas, land use changes (i.e. habitat loss, degradation and fragmentation) and climate change were identified as main drivers of population decline (Wilson and Maclean 2011; Stefanescu et al. 2011b). However, not all species are equally affected by these drivers: habitat specialists were found to decline more strongly than generalist species in temperate and Mediterranean regions (Warren et al. 2001; Stefanescu et al. 2011b) due to restricted trophic niches and specific habitat requirements and sometimes also lower dispersal power (Kotiaho et al. 2005; Stefanescu et al. 2011a).

Metapopulation theory is essential for our understanding of the persistence of populations in spatially structured landscapes (Hanski 1998). The viability of a metapopulation crucially depends on the number and size, configuration and quality of habitat patches, which harbour the essential resources for survival and reproduction (Hanski et al. 1994). The subpopulations of a metapopulation are interconnected by dispersal. This exchange of individuals between subpopulations allows re-colonisation of vacant habitats (Bowler and Benton 2005) or re-enforcement of local populations with low growth rates (i.e. rescue effect) (Brown and Kodric-Brown 1977). These processes make dispersal a crucial determinant for the functioning of metapopulations. Hence, a thorough understanding of dispersal is needed to efficiently establish conservation measures, such as functional corridors and stepping stones, which aim to improve the functional connectivity of a given landscape (Haddad 1999; Dennis et al. 2013).

The spatial configuration of patches (i.e. interpatch distance and matrix) defines the structural connectivity of a landscape (Baguette and Van Dyck 2007). However, to be informative, the dispersal abilities of a target organism must be considered to draw valid conclusions about the functional connectivity of a given landscape for a given organism (Stevens and Baguette 2008; Kadoya 2008; Öckinger et al. 2010). In this context, the quantification of dispersal kernels is an often applied technique to assess the distance-dependent reduction of the dispersing fraction of individuals. This technique allows the estimation of the probability of long-distance movements (Baguette et al. 2000; Baguette 2003; Junker and Schmitt 2010; Stevens et al. 2010), which are important for the functioning of metapopulations (Trakhtenbrot et al. 2005). Especially for butterflies, such analyses are important predictors of dispersal power, in particular if one is interested in short-term responses to habitat fragmentation and recent climate change (Stevens et al. 2010). In addition to changes in number, size and connectivity of habitat patches, land use changes also affect habitat quality, which is equally important for metapopulation viability (Thomas et al. 2001; Mortelliti et al. 2010). For grassland specialists, habitat quality is often negatively impacted over time by abandonment of traditional land use (such as extensive grazing or mowing of low productivity grasslands) or conversion of such areas into arable fields, urban or forested areas (Settele et al. 2009). Due to the ongoing farmland abandonment process in parts of southern Europe on the one hand and intensification of agriculture on the other, open habitats (such as semi-natural grasslands) belong to the most threatened habitat types throughout Europe (Habel et al. 2013). Open habitats have suffered the most pronounced butterfly population declines in recent years (Van Swaay et al. 2006; van Swaay et al.2013), emphasizing the urgent need to improve their conservation (Habel et al. 2013).

Currently, it is intensively debated, whether conservation decisions should either favour (1) connectivity conservation or (2) classic conservation measures [e.g. safeguarding the available (semi-)natural habitat, providing sufficient heterogeneity to buffer effects of climate change] (Hodgson et al. 2009, 2011; Doerr et al. 2011). For the decision whether connectivity or classic conservation measures should be applied, a profound understanding of the requirements of all life stages and the dispersal abilities of a given organism is essential. Classic strategies may be most useful if dispersal power is low or when barriers impede tracking of existing suitable environments. While such information is available for many of the endangered butterfly species in the UK or the Netherlands (Bink 1992; Asher et al. 2001), detailed information is still lacking for most species in the Mediterranean Basin.

To establish conservation strategies thorough autecological studies are urgently needed. Comparisons of occupied and unoccupied habitats can, for instance, help to identify relationships between patch characteristics and butterfly occupancy (Heer et al. 2013). Moreover, mark–release–recapture (MRR) studies provide information on butterfly population dynamics (i.e. size, recruitment and survival) and also dispersal abilities (e.g. Schtickzelle et al. 2002; Junker and Schmitt 2010; Zimmermann et al. 2011b). Such knowledge is essential for sound habitat management and the establishment of ecological networks (Thomas et al. 2010).

In this article, we investigate the autecology of the adult stage of *Euphydryas desfontainii* (Godart 1819), one of Portugal's rarest butterflies, where it is only found in very

restricted areas of the Lower Alentejo and Algarve provinces (Maravalhas 2003). The species is considered highly specialized (monophagous and high biotope specialisation in this particular region) and inhabits metapopulations with regular dispersal events (Stefanescu et al. 2011a), but so far we lack quantitative estimates of dispersal ability. We investigated the effects of landscape and habitat structure on habitat patch occupancy by *E. desfontainii*, its dispersal ability and demographic parameters. Based on our results, we suggest management strategies for the conservation of the species' marginal populations in southern Portugal.

Materials and methods

Study species

Euphydryas desfontainii belongs to the butterfly family Nymphalidae; it has a scattered distribution on the Iberian Peninsula and occurs only locally in adjacent France (Eastern Pyrenees). The species is also found in Northern Africa with localised populations in the Atlas Mountains (Morocco and Algeria). The subspecies *E. desfontainii baetica* (Rambur 1858) inhabits the southern parts of Spain and Portugal (Tolman and Lewington 1998). In Portugal, the adult butterflies are on the wing from April to June in one discrete generation (Maravalhas 2003). The species is found from sea level up to 1,800 m a.s.l. on hot rocky slopes (Tolman and Lewington 1998). Although the species can be classified as a typically Mediterranean faunal element, its habitats are characterized by some water availability. While populations in the most xeric regions are restricted to higher elevations with abundant precipitation [e.g. >500 m a.s.l. in the Middle Atlas mountains (Tolman and Lewington 1998)], humid meadows in valley bottoms are used in the low elevation populations of southern Portugal and south-western Spain (Novoa Pérez and García-Villanueva 1996; Pennekamp et al. 2013). The host plant is usually associated with soils characterised by fluctuating moisture content due to temporal inundations in winter and spring (Novoa Pérez and García-Villanueva 1996; Pennekamp et al. 2013).

The larval ecology is key to a successful conservation strategy for butterflies (Thomas et al. 2010). In a previous study, we investigated the larval ecology of *E. desfontainii* in the study region among and within patches (Pennekamp et al. 2013). Females choose large individuals of the locally used host plant, *Dipsacus comosus*; eggs are laid in clutches, but only on second year individuals. The surroundings of the plants chosen for oviposition also matter, as plants in small stands, with lower sward and more sunshine hours are selected indicating that specific microclimatic conditions are preferred (Pennekamp et al. 2013).

Study area

The study was conducted in the Algarve and the adjacent Lower Alentejo province (southern Portugal). The study area comprises a mosaic of extensively used meadows, maquis shrublands (mainly *Cistus ladanifer*) and some *Eucalyptus globulus* plantations (Krohmer and Deil 1999). The hilly topology (up to 300 m a.s.l.) is marked by small and temporary river beds with *Rubus* hedges and meadows used for extensive cattle grazing. The high clay content of the soils favours the retention of water in the lower parts and creates a suitable environment for the larval host plant, *D. comosus*. The Mediterranean climate is characterised by mild wet winters and long dry summers, with normally little rain between mid-April and mid-October. The mean annual temperature for the region ranges from 15.5 to 17.5 °C (Mabberley and Placito 1993).

For the analysis of the adult habitat structures, we studied a habitat network in the region between São Teotónio and Saboia in the Northwest and São Marcos da Serra in the East spanning about 200 km^2 (Fig. 1). For the capture–recapture study, we selected three sites close to Pereiras (central position at 37°25′N, 8°28′W), each of them having areas with host plants. The three sites were about 700, 1,400 and 1,700 m apart and had surface areas of 200, 1,400 and 16,500 m^2 separated by a matrix of extensively used meadows (i.e. used as cow pastures in most cases) and *Eucalyptus* plantations.

Adult habitat structures

To determine the habitat characteristics associated with the presence of butterflies, a systematic search for imagos was conducted in all known patches with the larval host plants at the peak abundance of butterflies in mid-April. The time searched for butterflies depended on patch size (<2,000 m^2: 20 min, >2,000 m^2: 40 min); the search was stopped as soon as an *E. desfontainii* butterfly was detected. Habitat patches were defined by the presence of *D.comosus* plants. Further environmental variables considered important for the species' presence were collected for occupied and unoccupied patches between 17 March and 2 April 2008: area of the patch of host plants (minimum 10 individuals, a distance of more than 100 m to the next plant was defined as a new patch), degree of shading (three categories), soil humidity (three categories), slope (measured in degrees and exposition), daily mean temperature, daily mean minimum and maximum temperatures (measured once per hour using data logger Tinytag Explorer [Gemini Data Loggers (UK) Ltd. 2004–2007]), number of host plants in the patch as well as cover of bare soil, herb and shrub layer in 5 % steps, the presence of water bodies and whether the area was used for grazing or not. Based on the centroid position of each patch, a

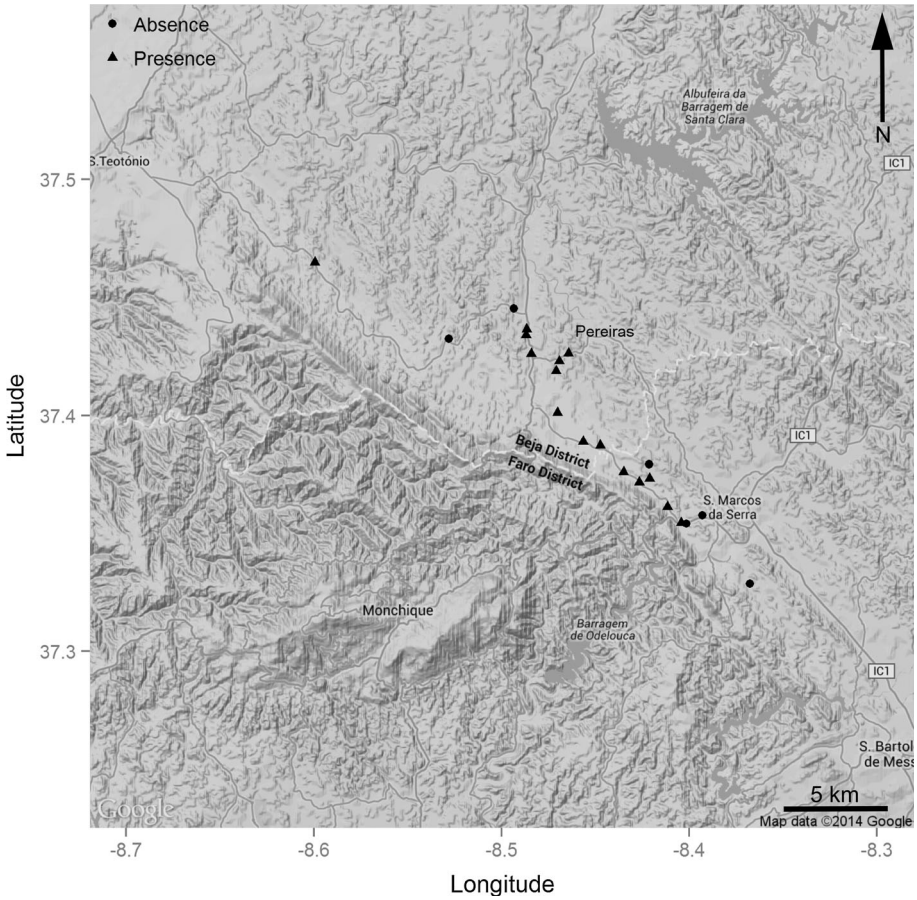

Fig. 1 Terrain map of the Algarve and Lower Alentejo regions between São Teotónio in the West and São Marcos da Serra in the East showing the study sites for the presence–absence analysis of *Euphydryas desfontainii* imagos

distance matrix between all patches was calculated and the minimum distance to the next patch and the next occupied patch was determined. Non-parametric Kruskal–Wallis tests were performed to compare occupied and unoccupied patches in terms of their characteristics for continuous and ordinal predictors, whereas the effect of grazing and the presence of water bodies on butterfly occupancy was tested with Fisher's Exact test. Additionally, non-metric multidimensional scaling was used to reveal multivariate relationships between patch features and butterfly occupancy and clustering tested using analysis of similarity (ANOSIM) implemented in the R package vegan (Oksanen et al. 2013). All statistical analyses were performed in the R—statistical computing environment (R Development Core Team 2012).

Mark–release–recapture study (MRR)

We performed a MRR study (18 sessions over 35 days) between 3 April and 8 May 2008 in three adjacent areas. Butterflies were captured by hand-netting between 9:30 am and 5:30 pm every day with suitable weather conditions (>20 °C, less than 50 % cloud cover and weak to moderate wind). One person (FP) criss-crossed the study areas and captured all encountered *E. desfontainii* individuals. First captured individuals were marked with a unique code by writing a number on both hind wings with a pen containing water- and light-resistant ink (Staedtler Lumoocolor S). Prior to releasing the butterfly at the point of capture, the exact position was recorded with a GPS (Magellan Meridian Platinum, measuring accuracy about 3 m). We also determined the sex of the individual and classified its wing wear on a scale from 1 to 4 (1 = fresh individual, 4 = heavily worn individual, cf. Konvička and Kuras 1999). We only obtained a sufficient number of recapture events for the largest of the three sites to estimate survival rates, catchability and population size. Analyses were done with the program MARK 6.0 (White and Burnham 1999) using the POPAN module (Schwarz and Arnason 1996): first, the survival rate (phi) and catchability (p) were determined by using the Cormack–Jolly–Seber (CJS) method testing for effects of time (constant or varying between sessions) and sex. The best CJS model (survival and catchability) was then used as the basis in the POPAN module to model survival, catchability and the recruitment (pent), and we further tested for linear or quadratic trends on survival and recruitment as well as interactive or additive effects of time and sex. Finally, we checked whether the sampling effort (hours spent in the sampling area) improved catchability estimation compared to the time effect (i.e. marking day). From the set of models, we choose the model best representing the data

set based on the Akaike Information Criterion corrected for small sample sizes (AIC_c), i.e. the model with the lowest AIC_c (Burnham and Anderson 2002; Johnson and Omland 2004), and we derived the daily population sizes and the super-population size from this model. We also recorded the use of nectar plants during the MRR study and provide a list of the species most frequently visited.

Mobility

We used the GPS data collected during the MRR study (i.e. capture events from all sites) to infer the movement behaviour of *E. desfontainii*. We calculated the distance between a capture and subsequent recapture event and assessed the dispersal kernels obtained for males and females by calculating the inverse cumulative proportion of individuals in distance classes of 100 m. The inverse power function (IPF) was fitted to the dispersal kernels in order to predict rare long distance movements (Baguette et al. 2000; Baguette 2003; Fric and Konvicka 2007): Applying the IPF, the cumulative proportion I is log-transformed and equates as:

$I_{IPF} = cD^{-n}$ respective $\ln(I) = \ln(c) - n \ln(D)$

The parameter c is a scaling constant while n is a parameter describing the effect of distance on the dispersal probability. The estimation of the parameter n is done by log-transforming the inverse cumulative proportion and regressing it against the log-transformed distance D. We evaluated potential sex differences on the intercept and the slope of the regressions by model comparisons based on the Akaike Information Criterion (AIC_c) (Burnham and Anderson 2002; Johnson and Omland 2004). Finally, the likelihoods for dispersal beyond distances measured in this study were extrapolated.

Results

Habitat requirements

The majority of patches was occupied (N = 16), while only five unoccupied patches were encountered. Regarding their univariate characteristics (Table 1), occupied patches only differed significantly in having about fourfold higher abundances of host plants. There was a trend of patches also being larger, however this was only marginally significant. Fisher's exact test did not reveal an association of water body presence nor grazing with patch occupancy. A multivariate analysis using non-metric multidimensional scaling to display patches according to their similarity and a subsequent ANOSIM detected no significant differentiation between occupied and unoccupied patches (Global R: 0.12, $p = 0.134$) (Supplementary material Figure S1).

Demography

During the MRR study, we marked 1,191 individuals (706 males, 485 females) of which 464 individuals were recaptured at least once in a total of 1,973 capture/recapture events. Males were recaptured considerably more often than females (46.1 vs. 28.4 %) (Table 2). The maximum observed survival (i.e. time from first capture to last recapture) was 26 days for males and 23 days for females. The mean number of observed survival days was 5.7 (±4.9 SD) for males and 5.4 (±4.3 SD) for females.

The capture–recapture data were best represented by a single model explaining more variation than all other models tested (Table 3). The difference (ΔAIC_c) to the second best model was 27.4 rendering the best model the only one with substantial empirical support (Burnham et al. 2011). According to the best model, the survival rate decreased over the flight season for both sexes following a linear trend declining from 0.88 for both sexes at the beginning to about 0.81 at the end. The catchability differed between sexes and varied with capture session. The effect of sex on catchability was additive with males always having higher capture rates (on average 0.38 for males vs. 0.29 for females). An alternative model where catchability was modelled by marking effort expressed as hours spent in the field instead of marking day decreased the fit of the best model ($\Delta AIC_c = 7.64$). The proportional recruitment of individuals to the population was represented by a quadratic term and an interaction with sex translating into a parabolic curve. Consequently, the number of individuals entering the population increased with time and decreased towards the end of the flight season with an earlier peak for males than for females. The peaks of male (16-4-2008) and female abundance (30-4-2008) were separated by about 14 days (Fig. 2). The super-population sizes, containing all individuals born into the population over the whole study period, were almost equal with 1,041 (±36 SE) males and 1,005 (±60 SE) females, which leads to a balanced sex ratio.

254 visits on flowering plants for nectar feeding were recorded. Most visits (48.4 %) targeted plants with yellow flowers belonging to the Asteraceae, particularly *Coleostephus myconis*, *Andryala integrifolia*, *Crepis versicaria* and *Reichardia picroides*. However, visits to blue or violet flowers of *Scabiosa atropurpurea* (17.4 %) and *Lavandula stoechas* (9.5 %) were also registered frequently.

Mobility

The movement behaviour was characterized by fractions of about 77 % males and 64 % females not moving more than 100 m in their lifetime. The mean distances of the life time movement of 150 m (±202 m SD) for males and 190 m

Table 1 Comparison of patch characteristics (median and interquartile range) in relation to *Euphydryas desfontainii* butterfly occupancy. In occupied patches, more host plants were found and there was a trend that occupied patches were larger. Statistically significant *p* values are shown in bold

Variables	Unoccupied patches (n = 5)		Occupied patches (n = 16)		*H*-test	*p*
	Median	Interquartile range	Median	Interquartile range		
Area (m^2)	328	329	1,863	3,386	3.79	0.052
Inclination (°)	0	0	0	2.5	0.24	0.625
Shading	3	0	3	1	1.00	0.317
Humidity	1	0	1	1	2.47	0.116
Mean temp (°C)	16.03	1.3725	16.905	1.275	1.96	0.161
Max. temp (°C)	18.83	2.435	19.57	2.89	0.02	0.876
Min. temp (°C)	13.255	0.66875	14.42	0.835	0.02	0.876
Number HP	37.5	86.75	160.5	240.25	5.64	**0.018**
Cover soil (%)	45	37.5	70	25	0.05	0.828
Cover herb (%)	48.75	38.125	20	22.5	2.50	0.114
Cover shrub (%)	0	3.75	0	5	2.74	0.098
Distance to nearest patch (m)	767	2,503	765	574	0.61	0.436
Distance to nearest occupied patch (m)	975	2,396	765	606	1.76	0.185

Table 2 Overview of the number of captures and recaptures of *Euphydryas desfontainii* butterflies and their average distances moved as observed in a MRR study

Sex	Marked individuals	Capture events	Recaptured individuals	Recapture ratio (%)	Longest move (m)	Mean move length (m)
Males	706	1,275	326	46.1	1,425	150 (±202)
Females	485	698	138	28.4	1,207	190 (±240)

Table 3 AIC_c model selection for *Euphydryas desfontainii* showing the ten best supported models. The best model considers equal survival rates for both sexes decreasing with time, the catchability differing between sexes and capture day and the proportional recruitment differing between sexes and including a quadratic term. The model best representing the capture-recapture data is shown in bold

Model	AIC_c	ΔAIC_c	AIC_c weights	Model likelihood	Parameters
{phi (tlin) p (g+t) pent (g*tlin+$tlin^2$) N (.)}	**4,163.205**	**0**	**1**	**1**	**28**
{phi (tlin) p (g+t) pent (g*t) N (.)}	4,190.635	27.43	0	0	57
{phi (tlin) p (g+t) pent (g+tlin+$tlin^2$) N (.)}	4,280.02	116.82	0	0	27
{phi (tlin) p (g+t) pent (g+t) N (.)}	4,296.033	132.83	0	0	41
{phi (tlin) p (g+t) pent (g) N (.)}	4,328.542	165.34	0	0	25
{phi (tlin) p (g+t) pent (tlin+$tlin^2$) N (.)}	4,329.166	165.96	0	0	26
{phi (tlin) p (g+t) pent (g+tlin) N (.)}	4,330.131	166.93	0	0	26
{phi (tlin) p (g+t) pent (g+tlin) N (.)}	4,330.131	166.93	0	0	26
{phi (tlin) p (g+t) pent (t) N (.)}	4,337.141	173.94	0	0	40
{phi (tlin) p (g+t) pent (tlin) N (.)}	4,351.529	188.32	0	0	25

(±240 m SD) for females were not significantly different (Kruskal–Wallis-test: 1.80, $p > 0.17$). The maximum distance moved was 1,207 m for females and 1,425 m for males. Six events where individuals changed among two of the three sites were registered: five of these exchanges were between the two sites separated by about 700 m, whereas only one exchange was found between the sites 1,400 m apart. No exchange between the 1,700 m distant sites was recorded.

Fitting the inverse cumulative proportion values of individuals moving certain distance classes to the IPF yielded a good fit for both sexes ($R^2 = 0.96$ and 0.90, for males and females, respectively; Table 4). An AIC_c model comparison suggested that most of the variation was explained by a model where sexes differed in their intercept, but not in the decay of the dispersing fraction with distance (Table 4). However, the second best model including an interaction between sex and log-distance had a ΔAIC_c of 2.16 and therefore still some empirical support (Table 5). Fitting the IPF function to each sex separately, the probability for a male to move beyond the distance of 500, 1,000 and 2,000 m was 0.063, 0.016 and 0.004, while

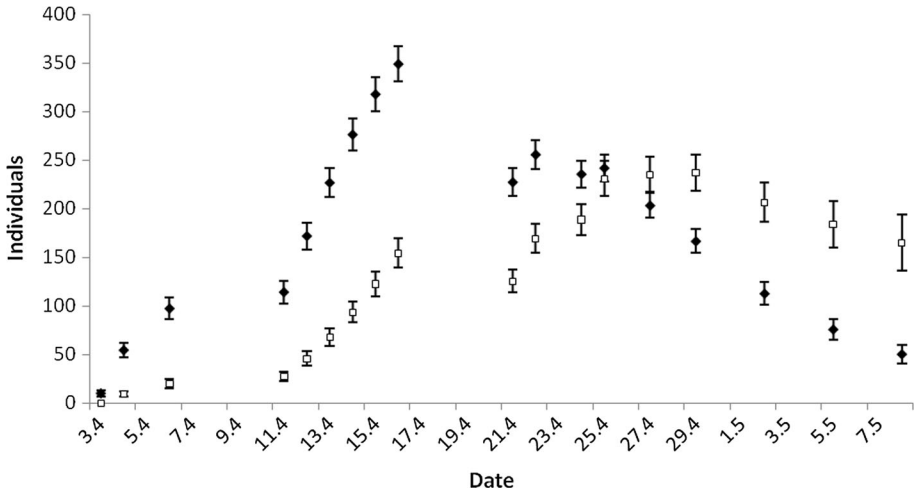

Fig. 2 Population sizes and *standard error bars* of *Euphydryas desfontainii* derived from the best supported model. Males (*filled diamonds*) appear before females (*open quadrats*), resulting in peak abundances shifted for about 2 weeks between sexes

Table 4 Parameters of the inverse power function separately estimated for both sexes of *Euphydryas desfontainii*

Sex	Formula	Stability index (R^2)
Males	$I = 16{,}706 * D^{-2.01}$	0.96
	$\ln(I) = 9.72 - 2.01 \ln(D)$	
Females	$I = 8{,}464 * D^{-1.83}$	0.90
	$\ln(I) = 9.04 - 1.83 \ln(D)$	

Table 5 AIC_c model selection to determine whether the regression of the log-transformed inverse cumulative proportion differs between sexes of *Euphydryas desfontainii*

Factors	No. of parameters	Log-likelihood	AIC_c	ΔAIC_c
log(distance) sex	4	−13.32	36.38	0.0
log(distance) sex log(distance)*sex	5	−12.91	38.54	2.16
log(distance)	3	−17.59	42.18	5.80
Intercept only	2	−51.69	107.8	71.47
Sex	3	−50.92	108.8	72.46

for the females the estimated probabilities were 0.097, 0.027 and 0.008, respectively (Fig. 3).

Discussion

Our study indicates that the habitat occupancy by adult stages of *E. desfontainii* was mainly influenced by host plant abundance and patch area. The imagos' dispersal power is moderate, largely coinciding with or even exceeding what is expected for checkerspot butterflies and potentially leading to occasional long-distance movements (i.e. distances of several kilometres). Based on our findings, we discuss consequences for the conservation of the species in the face of habitat and climate change.

Habitat requirements

We found that host plant abundance and patch size, the former often seen as a measure of habitat quality, are of prime importance for *E. desfontainii.* These findings match what is known for several other checkerspot butterfly species such as *Euphydryas aurinia* (Wahlberg et al. 2002b; Anthes et al. 2003). However, patches occupied by *E. desfontainii* did not differ significantly in vegetation structure, although less herb and especially shrub cover characterized occupied patches. In previous studies, sward height was found to be important in the sister species *E. aurinia* due to its influence on microclimatic conditions (Fowles and Smith 2006; Betzholtz et al. 2007). Encroachment of shrubs, in general, is known to have negative impacts on species living in grasslands and relying on the occurrence of herb species that require certain disturbance regimes (Thomas et al. 2010). Habitats often are suffering from encroachment when traditional land use practices are stopped because they are no longer commercially viable (Bourn and Thomas 2002).

In our study area, grazing by sheep and cattle is still practiced, but likely to vanish because people turn to more profitable jobs in the rapidly developing coastal region of the Algarve. Grazing did not influence occupancy status, although one would expect that grazing may have a positive effect on the ruderal host plant. However, our grazing evaluation was rather coarse (presence/absence), therefore a targeted study is needed to assess how grazing affects host plant abundance, vegetation structure and the resulting microclimatic conditions around host plants for successful larval development (Pennekamp et al. 2013), given that grazing can also negatively affect populations of rare specialist butterflies (Baguette et al. 2011).

In terms of structural connectivity, no differences were found between occupied and unoccupied patches meaning that the patches in our habitat network are probably still

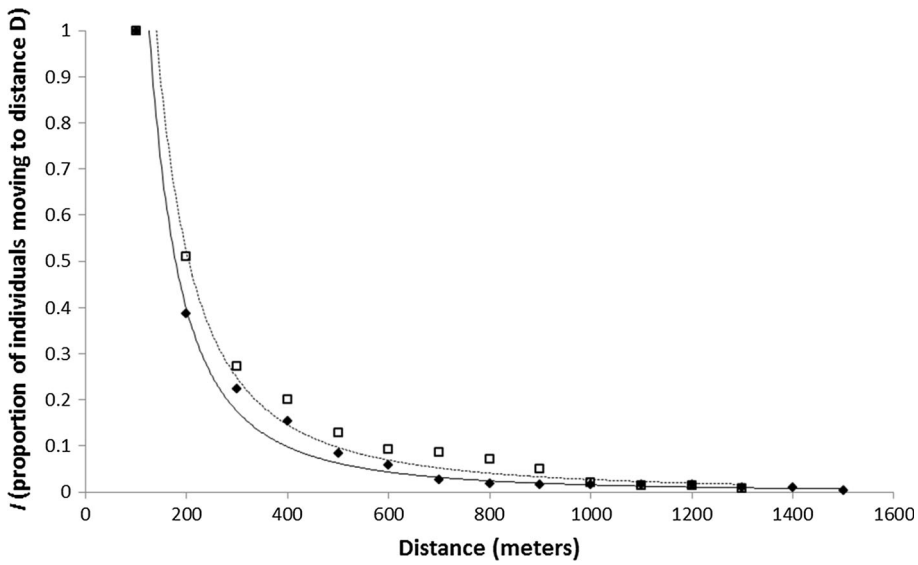

Fig. 3 Fitting an inverse power function to the inverse cumulative proportion of individuals of *Euphydryas desfontainii*. Observed proportions moving to the distance D are given as *symbols*, fitted IPF as *solid line* for males (*filled diamonds*) and *dashed line* for females (*open quadrats*)

sufficiently connected. The connectivity within the system of *E. desfontainii* habitats is important for the re-colonisation dynamics as suggested by metapopulation theory (Hanski 1998). Patch isolation was found to influence occupancy in a metapopulation of *E. aurinia* in Sweden (Betzholtz et al. 2007), while a study in Finland did not detect effects of isolation (Wahlberg et al. 2002a). Nevertheless, empty patches in the system may still be important as stepping stones facilitating movement through the matrix (Harrison et al. 1988). Overall, our findings here match the results of our previous study on the habitat requirements of *E. desfontainii* larval stages at the landscape level, where also the number of host plants mattered most (Pennekamp et al. 2013).

Demography

The overall demography of *E. desfontainii* showed the pattern of other checkerspot butterflies, with earlier emergence of males than females (i.e. protandry), a parabolic abundance curve and separate peaks between sexes as also exemplified by the well-studied species *Proclossiana eunomia* and *E. aurinia* (Munguira et al. 1997; Schtickzelle et al. 2005; Junker and Schmitt 2010; Zimmermann et al. 2011a). In general, protandry is commonly observed for a wide range of butterfly species, where freshly emerged females can then be mated immediately after hatching (Zimmermann et al. 2011a) hereby optimising the reproductive success of early hatching males. However, males and females did not differ in their survival rates, which decreased linearly with the progression of the flight period. Schtickzelle et al. (2002) argue for a direct relation between decrease in survival and decreasing availability of nectar sources, which might have caused elevated mortality along the flight season of *P. eunomia*. In our study area, this explanation is less likely as *E. desfontainii* used different plant species as nectar sources, unlike *P. eunomia* which exclusively relies on a single nectar source, i.e. *Polygonum bistorta* (Schtickzelle et al. 2002).

The estimation of population size showed that *E. desfontainii* can locally reach populations of several thousands of individuals, being at least temporarily the most abundant butterfly species in the study patch. From a conservation point of view, large population sizes protect populations against the detrimental effects of demographic and genetic stochasticity and inbreeding, which usually operate in small populations (Caughley 1994; Habel and Schmitt 2012). On the other hand, population sizes of several thousands of individuals do not necessarily protect invertebrate populations from extinctions, e.g. given the enormous fluctuations known for checkerspot butterflies [twofold to fivefold among years, Ehrlich (1992)], mainly caused by varying degrees of parasitism and environmental (e.g. weather) conditions (Ehrlich 1992; Ehrlich and Hanski 2004). Indeed, several parasitic wasps and flies are known to attack *E. desfontainii* (Stefanescu et al. 2009), and parasitised caterpillars were frequently observed in the field, suggesting that populations might be strongly impacted by parasitism potentially leading to considerable fluctuations among years. Given that only a single year was studied, it is unknown whether the observed population size was well within or at an extreme of the normal population size range.

Dispersal

Checkerspot butterflies are generally considered as being rather sedentary compared to other butterflies (Wahlberg

et al. 2002b). *E. desfontainii* is no exception shown by the large fraction of individuals not moving more than 100 m from their first point of capture. However, we observed maximum distances of more than 1 km for both sexes, thus being considerably higher than for populations of the sibling species *E. aurinia* in the same geographic region (Junker and Schmitt 2010) observed maximum move distances of 349 and 283 m; mean distances: 53 and 39 m, for males and females, respectively). Munguira et al. (1997) reported equally low mean and maximum values for an *E. aurinia* population in Spain. However, studies on *E. aurinia* from other European countries found longer mean and maximum movements, for instance in Sweden, with maxima of 650 m for females and 1,670 m for males (Betzholtz et al. 2007), while dispersal events of more than 10 km were reported from the Czech Republic (Zimmermann et al. 2011b).

While MRR studies, due to their often limited spatial scale can miss rare long-distance movements (Schneider et al. 2003), the fitting of certain phenomenological models [e.g. IPF, negative exponential function (NEF)] to butterfly dispersal kernels has been suggested for predicting their dispersal power (Hill et al. 1996; Baguette et al. 2000; Baguette 2003). These models were found to be more reliable than mere expert knowledge (Stevens et al. 2010) and provide conservation practitioners with the option to rank dispersal abilities of species, if dispersal data has been available. In general, IPF is preferred over NEF, even in case of a less good fit, due to its superiority in extrapolating rare long-distance events (Baguette et al. 2000; Baguette 2003) and its independence from marking effort (Fric and Konvicka 2007).

The dispersal kernel was best modelled with a lower intercept for females compared to males, which translates into lower overall mobility for the former, but a similar decay of dispersal distance for both sexes. However, the next best model including the interaction between sex and distance also had empirical support (ΔAIC_c 2.16). In terms of probability to move beyond the distance of 1 km, the IPF predicts a lower likelihood for males (0.016) than for females (0.027). Based on these values, *E. desfontainii* can be compared to species like *Boloria aquilonaris* with a probability of 0.021 for the same distance (Baguette 2003), or *E. aurinia* (males: 0.028; females: 0.029) and *Brenthis ino* (males: 0.024; females: 0.027) in the Czech Republic (Fric et al. 2010). Therefore, bridging distances between habitats of 1 km or even more should not represent a problem for maintaining the metapopulation structure in *E. desfontainii*.

Conservation implications

Strategies to face the challenges of climate and habitat change to safeguard threatened invertebrates are heavily debated (Hodgson et al. 2009, 2011; Doerr et al. 2011). While improving connectivity is frequently quoted as a recommendable measure in the context of climate change (Heller and Zavaleta 2009), Hodgson et al. (2011) argue that such a focus on simple connectivity may yield inferior results compared to the classic conservation strategies. They make the point that much more uncertainty is related with the concept of connectivity (e.g. in measuring dispersal, effects of population size etc.), while the positive effects of increasing habitat availability and improving habitat quality are well demonstrated. Interestingly, these authors suggest that focusing on habitat conservation is even more important under the assumption of shifting habitats due to climate change. While they aim at finding the best outcome for entire communities, the best strategy for a certain target species is additionally influenced by the availability of habitats in the surroundings and its dispersal power.

Our results on *E. desfontainii* show dispersal abilities that should allow re-colonisations all over our studied habitat network (e.g. several kilometres). Therefore, safeguarding the species' survival in southern Portugal likely requires conserving the remaining habitat patches and guaranteeing their habitat suitability and especially their microclimatic heterogeneity to provide buffering against macroclimatic changes. In addition, flower-rich meadows with yellow-flowering plants of the family Asteraceae form part of the adult habitat to provide nectar to foraging *E. desfontainii* butterflies. These recommendations are in line with a recent review of conservation priorities in the UK, which highlights that preserving and improving existing habitats and guaranteeing their integration in a habitat network is essential for the preservation of species and communities (Lawton et al. 2010).

In butterflies, habitat specialists are usually defined by their degree of host specialization (mono- vs. polyphagous) and their association with certain biotopes (Kotiaho et al. 2005; Stefanescu et al. 2011a). According to these criteria, we classify *E. desfontainii* as a habitat specialist given that the larval stages in the study area exclusively feed on a single host plant and the species is only found in specific grassland habitat types in Southern Portugal. The degree of specialisation often interacts with the dispersal ability, which in the case of *E. desfontainii* can be considered as intermediate. In a comparison of Finnish butterflies, Kotiaho et al. (2005) attributed the highest risk of extinction to habitat specialists with narrow larval and adult resources that in addition are characterized by low dispersal ability. Their conclusions suggest that the ecological characteristics of *E. desfontainii* potentially predispose this species to a high extinction risk, whereas the dispersal ability should be sufficient to maintain the connectivity of a metapopulation.

Hence, habitat changes and losses are more likely to negatively affect *E. desfontainii* population viability than is habitat fragmentation. In addition, negative effects are expected due to climate change: the predicted climatic changes might cause a loss of climatic suitability in about 95 % of its current distribution in the future (Settele et al. 2008). Although these predictions are potentially too high because parts of the distribution in arid regions of the Maghreb were not included in the species' distribution models (Barbet-Massin et al. 2010), most of the rare habitats with high soil moisture are unlikely to persist when climate change proceeds. For these reasons, we advocate our previous recommendations to focus on the remaining habitats and especially to guarantee their suitability by providing the conditions for host plants growing in diversified microclimates.

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